

2 MAIZE - THE PLANT AND ITS PARTS

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One of the greatest deterrents to an appreciation of plant morphology is the terminology used to describe various plant parts. This problem is compounded in the case of maize because of its relatively unusual structure. We all learn that plants have a vegetative body composed of stems, leaves and roots, and that flowers contain sepals, petals, pistils and stamens. Maize, however, has at least three kinds of leaves, two kinds of stems, two kinds of roots, and two kinds of flowers in which glumes, lemmas and paleas take the place of sepals and petals. Fortunately, these parts are arranged in a relatively simple fashion, so the task of mastering maize morphology is not as difficult as it might seem. In this article we will identify some of the most important parts of the maize plant and describe their organization. More detailed descriptions of the developmental morphology of maize have been provided by a number of investigators. Kiesselbach (1949, reprinted 1980) gives a good general picture of maize structure and development. The external morphology and the histology of the vegetative and reproductive shoots have been studied by Bonnett (1948, 1953), Sharman (1942) and Abbe and co-workers (Abbe and Phinney, 1951; Abbe et al., 1951), while the most comprehensive descriptions of the embryogeny are those of Randolph (1936) and Abbe and Stein (1954). A summary of the histology of the corn plant, written by Sass in 1955, has been reprinted in the recent edition of Corn and Corn Improvement (1976).

The organization of the plant body: Maize is a member of the grass family, the Gramineae, and as in all grasses, most of the plant body is leaf tissue (Fig. 1a). To appreciate the general organization of the maize plant it is helpful, therefore, to see it in a leaf-less state (Fig. 1b). Stripped naked, the maize plant is not very impressive. Its main stem, or culm, is a slender, segmented shaft similar to a stalk of bamboo or sugarcane. The enlarged joints along the stem, the nodes, mark the points of leaf attachment; the stem segment between nodes is called the internode. Each node bears a single leaf in a position opposite that of the neighboring leaf, giving the plant two vertical rows of leaves in a single plane (Fig. 1a; 2). This so-called distichous phyllotaxy is typical of all leaf-like appendages, wherever they occur on the plant.

Maize has unisexual, rather than bisexual flowers. Male (staminate) flowers are located at the apical tip of the main stem in the tassel, a branched inflorescence. Female (pistillate) flowers are found in one to several compact ears, located on the ends of short branches near the middle of the stem (Fig. 1b; 2).

This partitioning of male and female flowers in separate structures distinguishes maize from other cereals and is one of the principal reasons that its genetics has been so conveniently explored. Making controlled pollinations in maize requires little more effort than that involved in placing a bag over the tassel and ear shoot. To perform a controlled pollination in rice, wheat, barley and other cereals, it is necessary to emasculate each

Appendix A

flower used as a female parent, an especially tedious job when each flower yields only one seed.

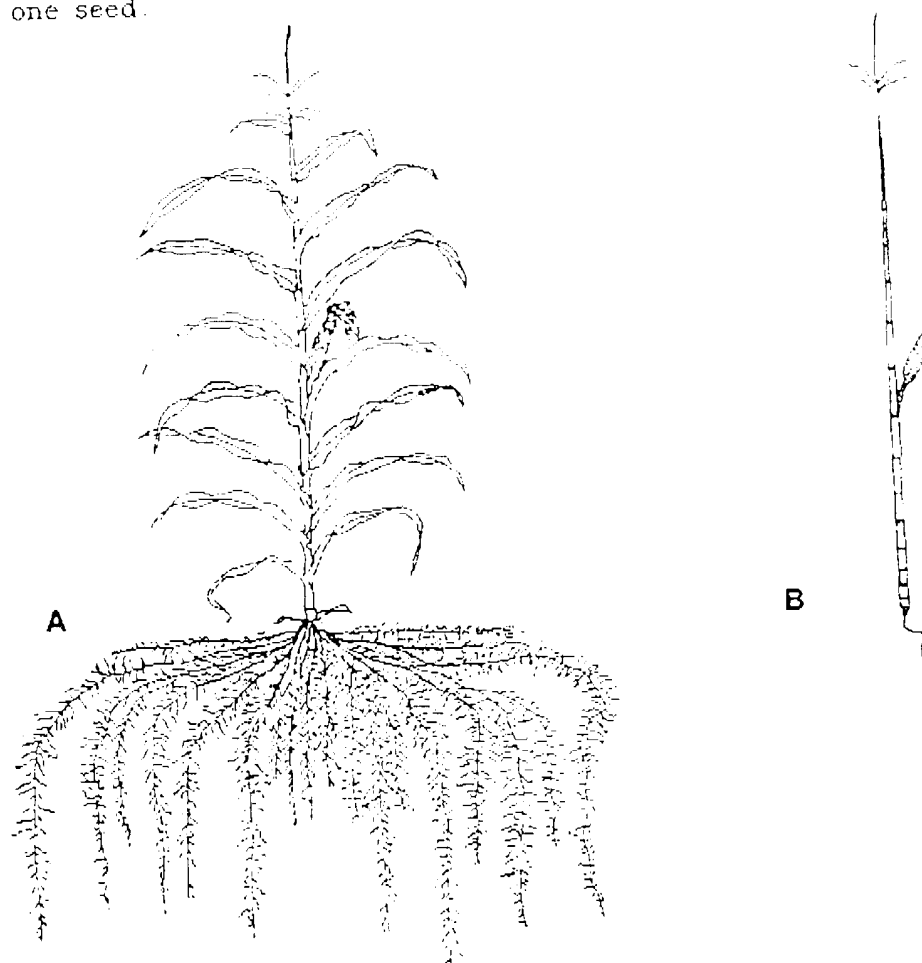


Figure 1. a) Mature maize plant (after Kiesselbach, 1949). b) Mature maize plant drawn without leaves and adventitious roots. The apical end of the main stem (culm) terminates in the tassel, while the basal end terminates in the primary root (radicle). The ear shoot arises from an internode near the center of the culm.

Maize also differs from closely related species in that it has relatively few branches. Only the lower 10 to 12 internodes of the stem produce branch primordia, and most of these remain suppressed. Above-ground primordia develop into ear shoots, while those located at subterranean internodes develop into tillers--branches identical in structure to the main stem. Commercial hybrids (except sweet corns) generally tiller very little, and typically produce a single viable ear shoot. In contrast, some "varieties" may have several large tillers and may produce 2 ears on the main stem and some ears on tillers.

The stem: During the first four weeks after germination, the growing point of the stem lays down all the nodes and internodes of the plant and then differentiates into a tassel. At the time of tassel formation the stem is not more than 3-4 inches tall, even though the plant may be 3-4 feet in

height (Fig. 3). Subsequently, the stem begins to elongate rapidly, with most of the growth occurring at the base of the internodes. The lowermost 6-8 internodes do not participate in this growth, however, and remain below ground where they produce the root system and tillers. These subterranean internodes taper sharply towards the base of the stem, forming a distinctive region, the crown (Fig. 1b). The stem is cylindrical above ground, and tapers gradually towards the tassel. All the internodes from the top ear downward have a distinct groove associated with the axillary bud at the base of the internodes; internodes above the ear lack axillary buds and are smoothly cylindrical.

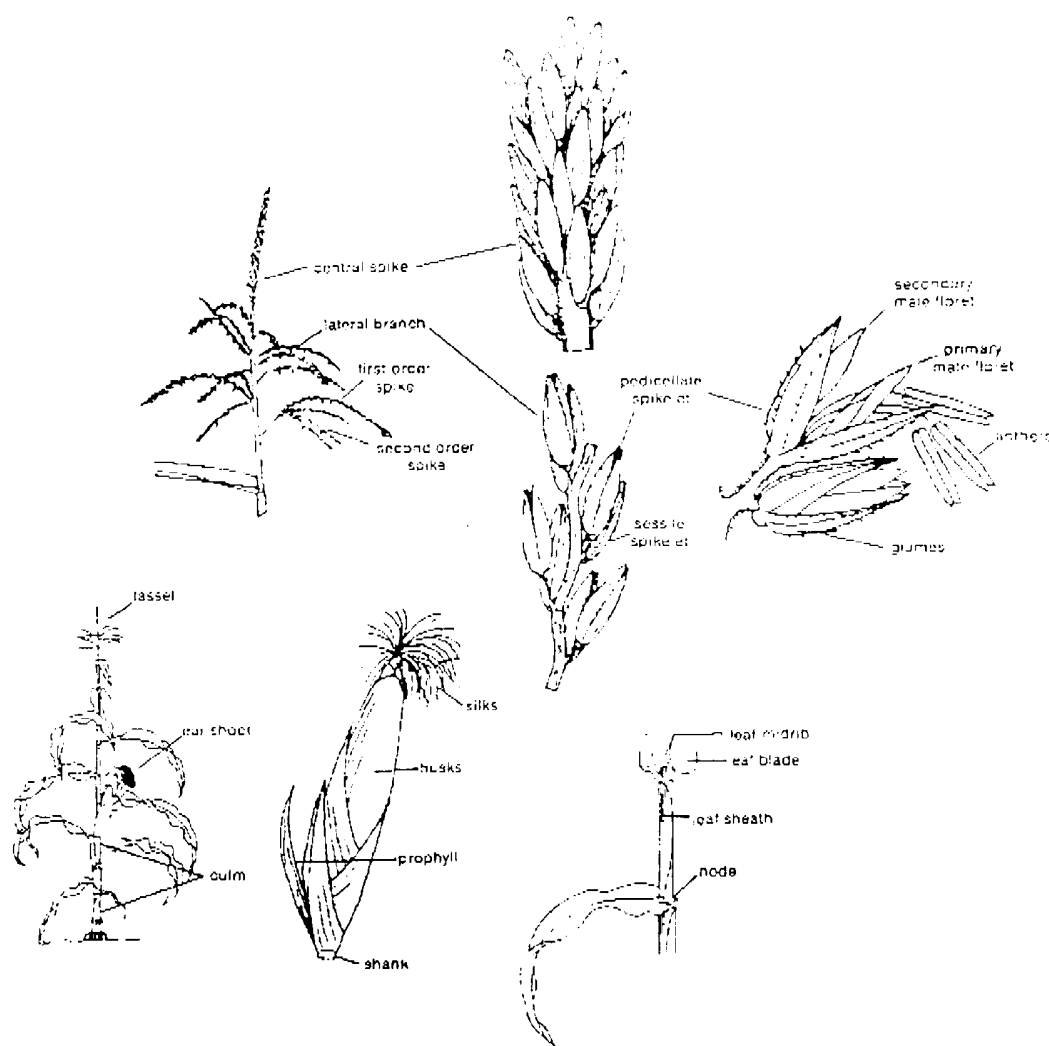


Figure 2. The major parts of the maize plant. Drawings in part from P. Weatherwax in *Corn and Corn Improvement*, 1955, and E. D. Styles *et al.* in *Can. J. Genet. Cytol.* 15:59, 1973; figure assembled by M. M. Johri and E. H. Coe.

The stem of an ear shoot, called the shank (Fig. 2), differs from the main stem in being relatively short in most strains. In addition, the internodes of the shank are variable in number, irregular in shape and size, and the surface is shielded rather than smooth surface. Secondary ear shoots commonly occur on the shank of several types of maize, but are not common in commercial strains unless fertilization of the apical ear is prevented.

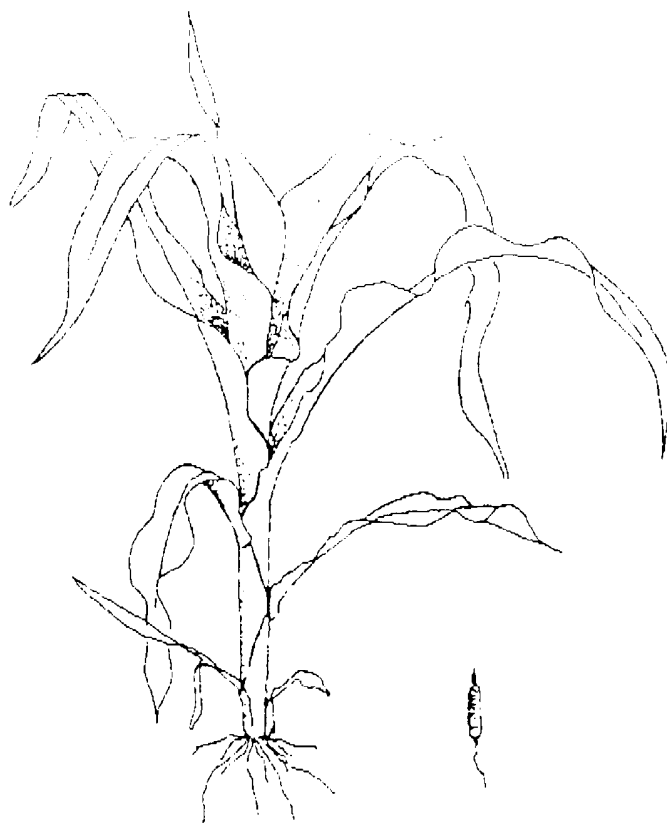


Figure 3. A four week old plant (approximately 3 feet tall) in which the stem apex has differentiated into a tassel. As shown on the right, the stem is still relatively short at this stage.

The tassel: The tassel, located at the top of the culm, consists of a series of large branches (spikes) covered with numerous, small flower-bearing branches (spikelets; Fig. 2). Each branch point on a spike bears two spikelets, one on a long stem (pedicellate), the other on a short stem (sessile) (Fig. 4a). Each of these spikelets, in turn, produces two functional florets. Although tassel florets contain both stamens and a pistil, the pistil normally degenerates soon after it is initiated, making the floret functionally male. However, pistils will develop at the base of the tassel under some environmental and physiological conditions, and are quite common on tillers.

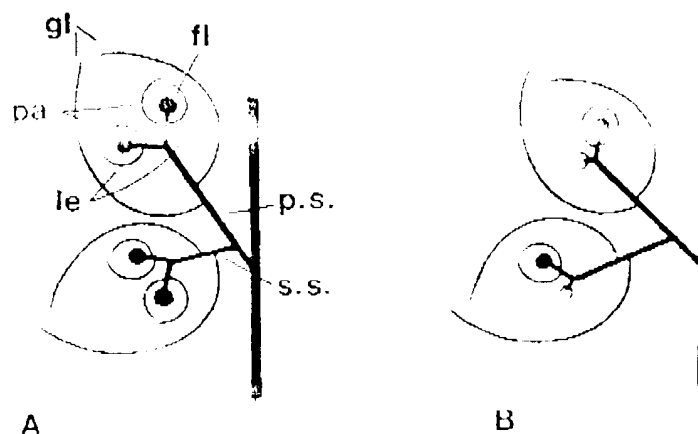


Figure 4. Schematic drawing of a pair of tassel spikelets (A) and a pair of ear spikelets (B). Note that the lower floret in the ear spikelet aborts early in development. p.s. - pedicellate spikelet; s.s. - sessile spikelet; gl - glumes; le - lemma; pa - palea; fl - floret.

Surrounding both florets on a spikelet are 2 leaf-like scales called glumes (Fig. 2; 4a). Within the glumes, each floret is individually enclosed in another pair of scales, one located adjacent to the glume (the lemma), the other located between the two florets (the palea) (Fig. 4a). At anthesis, these scales are forced apart by the swelling of conical structures (lodicules) at the base of the 3 stamens, and the filamentous base of the stamens elongates, forcing the anthers out of the flower (Fig. 2). As they dangle downwards, the anthers shed pollen from openings at their tip.

Pollen grains are the multicellular products of the haploid microspores that result from the meiosis of a microspore mother cell (microsporocyte). Meiosis takes place in the anther before the tassel emerges from the leaf sheaths. After meiosis, the 4 resulting haploid microspores separate from each other, and each forms a thick wall. Shortly before shedding, each microspore undergoes two mitotic divisions. The first division is asymmetric, and produces a relatively large vegetative cell and a smaller generative cell. In the second division, the generative cell divides to form two sperm cells.

The ear: The ear is morphologically similar to the tassel, although this resemblance is obscured by differences in the relative size of their parts. The crucial difference between them is, of course, that the tassel contains male flowers, and the ear bears female ones. This difference is due simply to the fact that during the formation of an ear floret, stamen primordia are arrested at an early stage in their development, while the pistil develops fully. Each functional ear floret has a single ovary, which terminates in an elongated style, or silk (Fig. 5). Within the ovary is a single embryo sac. The embryo sac is the product of one of the four haploid cells resulting from the meiosis of the megaspore mother cell. While its three sister cells degenerate, the nucleus of this cell divides three times to produce 8 haploid nuclei within a common cytoplasm (the embryo sac). Two of these nuclei (polar nuclei) migrate to the center of the embryo sac where they become closely associated. The three nuclei remaining at the base of the embryo sac

subsequently undergo cellularization to form the egg cell and two synergids, while the 3 nuclei at the tip of the embryo sac proliferate to form 24-48 antipodal cells.

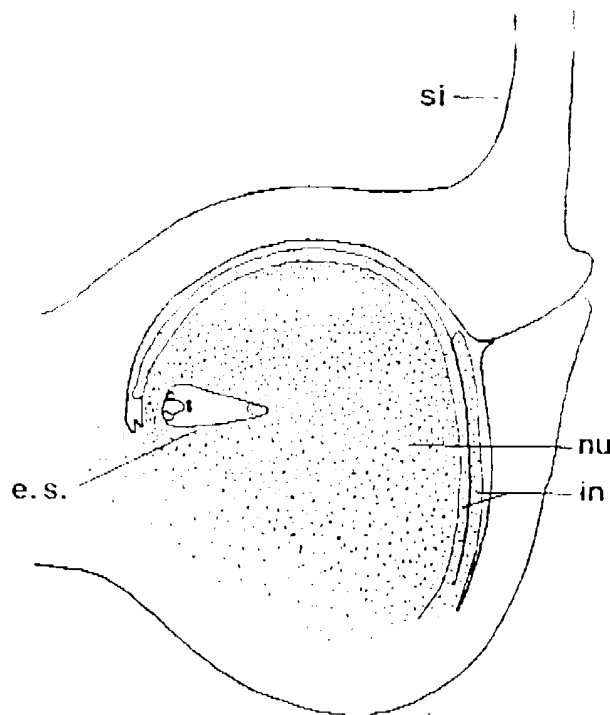


Figure 5. Radial longitudinal section of an ovary with an unfertilized embryo sac (after Randolph, 1936). Upon fertilization, the nucellus is digested by the expanding embryo sac and the tissue surrounding the nucellus is transformed into the pericarp. si - silk; e.s. - embryo sac; nu - nucellus; in - integuments.

The ear also differs from the tassel in that it has no major lateral branches. Its thick, lignified axis, the cob, is homologous to the central spike of the tassel. As in the tassel, ear spikelets come in pairs, but in the ear they are equal in size and only one of the florets in each spikelet is functional (Fig. 4b). An ear therefore has an even number of parallel rows of equally sized kernels equal to the number of spikelets on the cob. The number of rows (or ranks) of kernels ranges from 4 to 30.

The glumes, lemmas and paleas of the ear spikelets are readily visible in an unfertilized ear, but are soon obscured by the enlargement of the ovary after fertilization. In a mature ear these structures are represented by the chaff that adheres to the cob and the base of the kernel after it is shelled.

The leaf: Maize produces three kinds of vegetative leaves: foliar leaves, husk leaves and prophylls. A foliar leaf is located at each of the nodes on the main stem, husk leaves are located on the shank of the ear shoot, and prophylls are found at the base of the shank between the ear shoot and the stem (Fig. 2).

The foliar leaf has two distinct parts--the blade, a flat portion extending away from the stem, and the sheath, a basal part that wraps tightly around the stem (Fig. 2). Internally, the blade consists of a spongy network of cells traversed by a series of parallel, longitudinal veins. This flexible lamina is supported by the midrib, a thickened, translucent structure located in the center of the leaf. The sheath is thicker and more rigid than the blade, possesses fewer longitudinal veins, and lacks a prominent midrib. The sheath completely encircles the internode above the node to which it is attached and may extend the entire length of that internode. During the early development of the plant, the leaf sheaths provide most of the mechanical support necessary to keep the stem upright. At the boundary between the blade and the sheath there is a distinct hinge of translucent tissue. In this region the leaf blade and leaf sheath narrow sharply, forming an indentation in the leaf margin. The wedge of translucent tissue adjacent to this indentation is known as the auricle. The ligule is the thin collar of filmy tissue located on the inside of the hinge.

The husk leaves surrounding the ear are usually considered modified leaf sheaths, with vestiges of the blade portions occasionally present. In some strains husk leaves develop a prominent ligule and leaf blade. In contrast to the leaf sheath, husk leaves are relatively thin and flat. Each husk leaf is attached to a unique node on the shank, and all but a few upper ones are arranged distichously.

Located between an ear shoot and the stem, the prophyll looks superficially like a husk leaf, but is distinguished by having two keels (midribs) and a split apex. These features suggest that the prophyll arose evolutionarily from the fusion of two foliar leaves. The homology of the prophyll is still controversial, however. Galinat (1959), for example, considers the prophyll one of the basic units of maize morphology, the others being the internode, leaf and axillary bud.

The root: More is known about the growth, cell biology, physiology and anatomy of the primary maize root, or radicle, than perhaps any other organ of the plant. Its histological structure, described by Sass (1976) and Kiesselbach (1949), is typical of roots in general. The apex of the root is sheathed in a loose network of root cap cells. Immediately behind the apex is a zone of cell division and elongation, beyond which root hairs are initiated. Larger lateral roots arise at varying points behind the zone of root hair formation. Cell division is restricted to the apical 3 mm of the root, and occurs at a maximal rate 1.25 mm behind the apex. The zone of elongation extends 8 mm behind the apex, the rate of elongation being maximal 4 mm from the tip (Erickson and Sax, 1956). Those interested in using the root for physiological or cell cycle studies should consult Silk and Erickson (1979; 1980) and Green (1976) for an analysis of the growth parameters that must be taken into consideration in such studies.

The primary root represents the basal end of the plant axis, which in maize and other grasses contributes relatively little to the ultimate root system (compare Fig. 1a and b). Most of the root system consists of adventitious roots produced by the basal-most internodes of the stem. The primordia of a few adventitious roots are normally present in the embryo, and these emerge soon after germination. New root primordia are subsequently initiated at the base of all subterranean internodes, and also appear

at 2 or 3 above-ground internodes after the stem has elongated. Subterranean adventitious roots are sometimes called crown roots, while those initiated above ground are known as brace roots.

Adventitious roots grow horizontally for several feet before turning downwards. As a result, the root system of a corn plant in a mature region 6-8 feet in diameter, while the depth of the root system may be as much as 6 feet. As it grows, the root branches profusely in the region behind the apex, forming both secondary roots and unicellular root hairs. The total length of root system of a mature plant has been estimated to be 6 miles.

The kernel: The events surrounding the process of fertilization have been described by Miller (1919), Kiesselbach (1949) and Pfahler (1955); unfortunately, ultrastructural information about this phenomenon is still unavailable.

The silk is receptive to pollen along its entire length. Within 5 minutes after a pollen grain lands on a silk it sends out a tube which penetrates the silk and grows downward towards the ovary. During this process the vegetative nucleus and the two sperm cells migrate to the tip of the pollen tube where they remain throughout its growth. Upon reaching the embryo sac, 12 to 24 hours after germination, the end of the pollen tube bursts, releasing the two sperm. One sperm nucleus fuses with the two polar nuclei in the center of the embryo sac to form a triploid cell that gives rise to the endosperm. The other sperm nucleus fuses with the egg nucleus to form the zygote. As often as 2% of the time the polar nuclei and the egg nucleus are fertilized by sperm from different pollen grains, with the extra sperm nuclei being somehow lost (Sarkar and Coe, 1971). This phenomenon, called heterofertilization, can lead to a non-correspondence between the genotype of the endosperm and embryo when the male parent is heterozygous.

The development of the kernel following fertilization has been described in detail by Randolph (1936). We will only note here that this process takes 40-50 days and is accompanied by a 1400-fold increase in the volume of the embryo sac. The growth of the embryo and the accumulation of food reserves in the endosperm is completed by about day 40, and the remaining 10-20 days is spent maturing and drying.

A mature kernel has three major parts: the pericarp, endosperm and embryo (Fig. 6). The pericarp, the tough transparent outer layer of the kernel, is derived from the ovary wall and is therefore genetically identical to the maternal parent. The endosperm and embryo represent the next generation.

The endosperm makes up about 85% of the weight of the kernel and is the food source for the embryo for several days after it germinates. This food takes the form of intracellular starch grains and protein bodies, and is concentrated to varying degrees in different parts of the endosperm (Duvick, 1961). In flint-type kernels the concentration of starch and protein bodies is higher around the periphery of the endosperm than in the center, giving the endosperm a hard, corneous external layer, and a soft, granular center. In dent kernels, the granular tissue extends to the crown of the endosperm so that it collapses upon drying and produces a distinct indentation. These two traits are polygenic in their inheritance and are

characteristic of specific races of maize. Other common endosperm traits, such as sugary, floury or shrunken, are single gene mutations and can exist in either a flint or dent background.

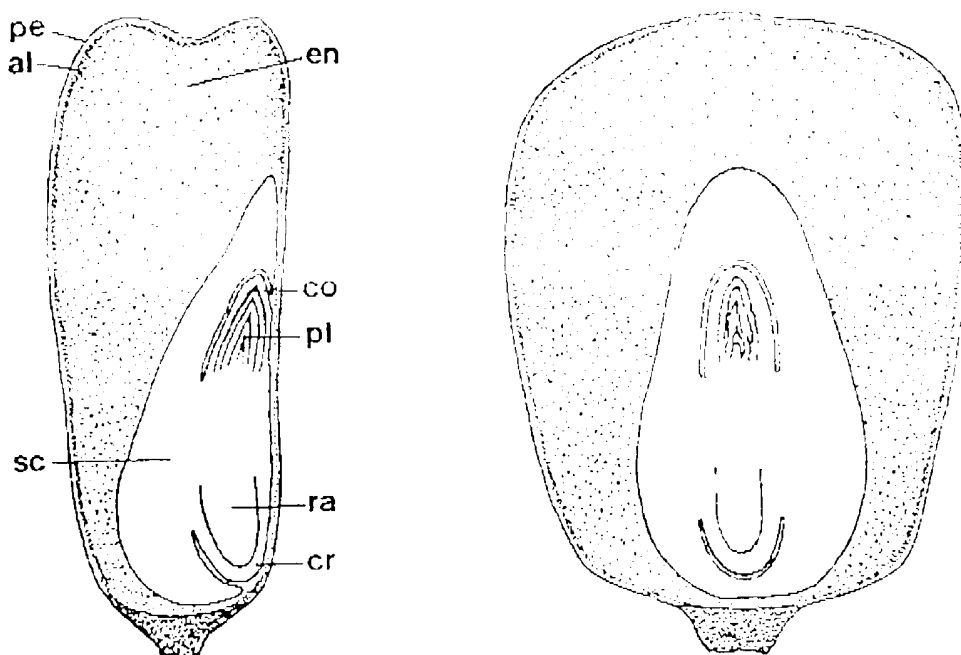


Figure 6. Longitudinal sections of a mature dent kernel, taken perpendicular (left) and parallel (right) to the upper face of the kernel (after Kiesselbach, 1949). pe - pericarp; en - endosperm; al - aleurone; sc - scutellum; co - coleoptile; pl - plumule; ra - radicle; cr - coleorhiza.

Much of our understanding of gene action in maize is based on the analysis of genes affecting the pigmentation of the external layer of the endosperm, the aleurone. This specialized single cell layer is the only part of the endosperm capable of becoming intensely pigmented. Internal endosperm cells may be either yellow or white.

The embryo is located on the broad side of the kernel facing the upper end of the ear, beneath a thin layer of endosperm cells. Most of the tissue in the embryo is part of the scutellum, a spade-like structure concerned with digesting and transmitting to the germinating seedling the nutrients stored in the endosperm. The shoot and root axis are recessed in the outer face of the scutellum. In a mature kernel, the shoot (plumule) has 5 to 6 leaf primordia that are arrested at successive stages of development (Abbe and Stein, 1954). Surrounding the shoot is a cylindrical structure called the coleoptile. Upon germination, the coleoptile elongates until it is above ground and is then ruptured by the more rapid expansion of the rolled leaves within it. The root is enclosed in a sheath of tissue called the coleorhiza. Unlike the coleoptile, the coleorhiza does not elongate very much, and gives way to the radicle as soon as it emerges from the seed.

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